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Laccariopsis, a new genus for *Hydropus mediterraneus* (*Basidiomycota, Agaricales*)

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Abstract — *Laccariopsis* (*Agaricales*) is a new monotypic genus established for *Hydropus mediterraneus*, an arenicolous species earlier often placed in *Flammulina*, *Oudemansiella*, or *Xerula*. *Laccariopsis* is morphologically close to these genera but distinguished by a unique combination of features: a *Laccaria*-like habit (distant, thick, subdecurrent lamellae), viscid pileus and upper stipe, glabrous stipe with a long pseudorhiza connecting with *Ammophila* and *Juniperus* roots and incorporating plant debris and sand particles, pileipellis consisting of a loose ixohymeniderm with slender pileocystidia, large and thin- to thick-walled spores and basidia, thin- to slightly thick-walled hymenial cystidia and caulocystidia, and monomitic stipe tissue. Phylogenetic analyses based on a combined ITS-LSU sequence dataset place *Laccariopsis* close to *Gloiocephala* and *Rhizomarasmius*.

Key words — *Agaricomycetes, Physalacriaceae,* /gloiocephala clade, phylogeny, taxonomy

Introduction

Hydropus mediterraneus was originally described by Pacioni & Lalli (1985) based on collections from Mediterranean dune ecosystems in Central Italy, Sardinia, and Tunisia. Previous collections were misidentified as *Laccaria maritima* (Theodor.) Singer ex Huhtinen (Dal Savio 1984) due to their laccarioid habit. The generic attribution to *Hydropus* Kühner ex Singer by Pacioni & Lalli (1985) was due mainly to the presence of reddish watery droplets on young lamellae and sarcodimitic tissue in the stipe (Corner 1966, Singer 1982). As this puzzling taxon combines features of several genera within *Physalacriaceae* Corner, the taxonomic position of this species has since been greatly debated and is still far from clear. Contu (1986, 1988) and Robich (1986) retained the taxon in *Hydropus*, but within a brief period, the specific epithet was recombined three times: Horak (1988) transferred it to *Oudemansiella* Speg., mainly because the pileipellis is embedded in a gelatinous matrix, the

stipe is rooting (pseudorhiza), and the basidia and spores are large and thick-walled; Bas & Robich (1988), after demonstrating that stipe tissue in the species is monomitic and clearly not sarcodimitic, treated the species as a *Flammulina* P. Karst., a placement also followed by Bon (1999) and Petersen et al. (2012); and Quadraccia & Lunghini (1990) and Ballero & Contu (1990) transferred it to *Xerula* Maire, where Contu (2000) designated *X. mediterranea* as the type of *Xerula* subg. *Ixoflammula* Contu.

Petersen (2000) and Antonín & Noordeloos (2010) felt that the species might better be placed within *Rhizomarasmius* R.H. Petersen, whose members share with *H. mediterraneus* common features such as a marasmioid habit with a deep rooting stipe, similar pileipellis and stipititrama structure, protruding cystidia, and monomitic trama. But, without molecular evidence, these authors refrained from transferring it to *Rhizomarasmius*.

In their thorough monograph on the *Xerula*/*Oudemansiella* complex (*Physalacriaceae*, Moncalvo et al. 2002, Matheny et al. 2006), Petersen & Hughes (2010) recognized seven genera based on both morphological and molecular data: *Dactylosporina*, *Hymenopellis*, *Mucidula*, *Oudemansiella* s.s., *Paraxerula*, *Ponticulomyces, Protoxerula*, and *Xerula* s.s.; *Hydropus mediterraneus* is not treated in the main taxonomic section (no collection is molecularly studied) but only discussed in the "Type specimen studies" section. Petersen & Hughes (2010) designated as neotype for *H. mediterraneus* a collection by M.M. Moser from Tuscany (no. 94/410, IB), but we have since verified that the holotype collection is housed in AQUI, as correctly indicated in the protologue.

Since *Hydropus mediterraneus* had not been molecularly studied and remained problematic relying only on traditional taxonomical methods, the aim of this paper was to infer the phylogenetic position of the species by using a combined ITS and LSU rDNA analysis.

Materials & methods

Herbarium acronyms follow Thiers (2012) except AP that refers to the personal herbarium of Alessio Pierotti. Author citations follow Index Fungorum (2012). The new genus and new combination are deposited in MycoBank (2012).

DNA extraction, PCR amplification, and DNA sequencing

Genomic DNA was isolated from 1 mg of one herbarium specimen (MCVE 23445), by using the DNeasy Plant Mini Kit (Qiagen, Milan Italy) according to the manufacturer's instructions. Universal primers ITS1F/ITS4 were used for the ITS region amplification (White et al. 1990, Gardes & Bruns 1993) and primers LR0R/LR7 (Vilgalys & Hester 1990; Vilgalys lab 2012) for the LSU rDNA amplification. Amplification reactions were performed in a PE9700 thermal cycler (Perkin-Elmer, Applied Biosystems) following Vizzini et al. (2011). The PCR products were purified with the AMPure XP kit (Beckman) and sequenced by MACROGEN Inc. (Seoul, Republic of Korea). The sequences were submitted to GenBank (2012) and their accession numbers are reported in Figure 1.

Sequence alignment and phylogenetic analysis

The sequences obtained in this study were checked and assembled using Geneious v5.3 (Drummond et al. 2010), and compared to those available in the GenBank database using the blastn algorithm. Based on the blastn results, sequences were selected according to the outcomes of recent phylogenetic studies on *Physalacriaceae* (Binder et al. 2006, Matheny et al. 2006, Petersen & Hughes 2010 and Ronikier & Ronikier 2011). A combined analysis of ITS and LSU sequences was carried out using, when possible, sequences from the same strain or specimen. *Armillaria mellea* (AY789081, AY700194) and *A. tabescens* (AY213590, AF042593) were used as outgroup taxa according to Binder et al. (2006), Matheny et al. (2006), and Ronikier & Ronikier (2011). Alignments were generated using MAFFT (Katoh et al. 2002) with default conditions for gap openings and gap extension penalties. The sequence alignment, its manual adjustment, and the best-fit models estimation follow Vizzini et al. (2011). The GTR+G and GTR+G substitution models was used in the ITS and LSU analysis, respectively. A partitioned matrix was used in all the analyses. Molecular-phylogenetic analyses were performed using the Bayesian Inference (BI) and Maximum Likelihood (ML) approaches. BI using Monte Carlo Markov Chains (MCMC) was carried out with MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001). Four incrementally heated simultaneous MCMC were run over 10.000.000 generations, under model assumption. Trees were sampled every 1.000 generations resulting in an overall sampling of 10.001 trees. The "burn-in" value was evaluated using Tracer 1.5 (Rambaut & Drummond 2007). The first 20% of trees was discarded as "burn-in". For the remaining trees, a majority rule consensus tree showing all compatible partitions was computed to obtain estimates for Bayesian Posterior Probabilities (BPP). ML estimation was performed through RAxML v.7.0.4 (Stamatakis 2006) with 1.000 bootstrap replicates (Felsenstein 1985) using the GTRGAMMA and GTRGAMMA (for ITS and LSU, respectively) algorithm to perform a tree inference and search for a good topology. Support values from bootstrapping runs (MLB) were mapped on the globally best tree using the "-f a" option of RAxML and "-x 12345" as a random seed to invoke the novel rapid bootstrapping algorithm. Only BPP values over 0.60 and MLB over 50% are reported in the resulting tree (Fig. 1).

Results

Molecular results

The combined dataset, which comprises 33 taxa (including 32 from GenBank), is 1883 base pairs long. As both Bayesian and Maximum likelihood analyses produced the same topology, only the Bayesian tree with both BPP and MLB values is shown (Fig. 1).

Both analyses cluster *Hydropus mediterraneus* within a clade (here indicated as the /gloiocephala clade, BPP 0.97, MLB 69%) formed also by four *Gloiocephala* species (including *G. epiphylla* Massee, the type of the genus) and two *Rhizomarasmius* species. This clade is sister to a group here indicated as the /xerula clade (BPP 1, MLB 96%) including *Strobilurus* Singer and *Xerula* s.s.

As traditionally circumscribed, *Gloiocephala* Massee is polyphyletic, as already pointed out by Binder et al. (2006) and Ronikier & Ronikier (2011).

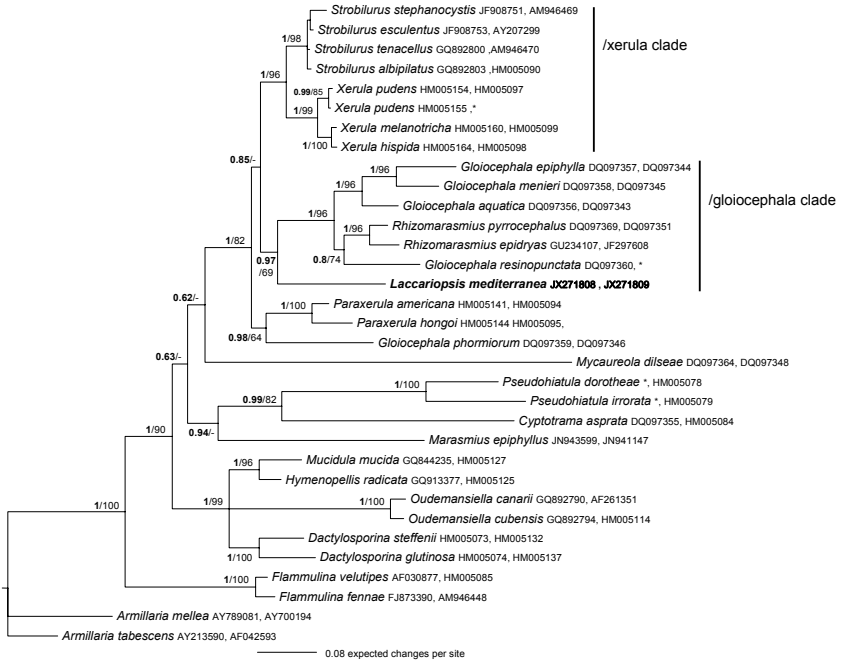

Figure 1. Bayesian phylogram obtained from the combined ITS-LSU sequence alignment. Support values for clades that are supported in either the Bayesian (Posterior Probabilities values – BPP) and Maximum likelihood (ML Bootstrap percentage – MLB) analyses are indicated. Only BPP values over 0.60 (in bold) and MLB values over 50% are given above branches.

Taxonomy

Laccariopsis Vizzini, **gen. nov.**

MycoBank MB 800949

≡ *Xerula* subg. *Ixoflammula* Contu, Micol. Veget. Medit. 15(1): 22 (2000).

A Rhizomarasmio *et* Gloiocephala *differt habitu* Laccariae *vel* Omphalinae, *pileo viscido, pili cute laxe hymenodermica, basidia, cheilo- atque pleurocystidia crassotunicata et in stuctura molecularis (ITS-spatiis internis transcriptis et LSU DNA).*

Type species — *Hydropus mediterraneus* Pacioni & Lalli

Etymology — named in reference to its *Laccaria*-like habit.

Basidiomata agaricoid resembling those of *Laccaria* spp.; lamellae thick, stipe deeply rooting (with long pseudorhiza), slightly viscid, pruinose only at apex, veils absent, spore-print whitish; spores large, thin- to thick-walled, smooth, inamyloid; basidia large, thin- to thick-walled (sclerobasidia); cheilo- and pleurocystidia abundant, thin- to thick-walled; pileipellis strongly gelatinized, made up of a loose hymeniderm with slender, cryptic, thin to moderately thick-walled pileocystidia; stipitipellis with caulocystidia, localized only at apex, thin- to slightly thick-walled; stipititrama monomitic; clamp-connections present.

Figure 2. *Laccariopsis mediterranea*.
Basidiomata on sand (from MCVE 23445). Photo by Matteo Carbone. Bar = 1 cm.

Rhizomarasmius and *Gloiocephala* differ in having a dry stipe, a dense hymeniform pileipellis, thin-walled spores, and shorter and thin-walled basidia; *Flammulina* differs in having a dry entirely velutinous stipe, smaller and usually thin-walled spores and basidia, usually thin-walled cheilo- and pleurocystidia, and well-developed pileocystidia; *Strobilurus* is distinguished by a dry pileus and stipe, a dense hymeniform pileipellis, a sarcodimitic stipe trama, and absence of clamp-connections; *Xerula* is characterized by a dry and velutinous pileus and stipe, a pileipellis consisting of a dense hymeniderm, pigmented and very thick-walled pileosetae, similar caulosetae, and a sarcodimitic stipe trama.

Laccariopsis mediterranea (Pacioni & Lalli) Vizzini, **comb. nov.** Fig. 2

MycoBank MB 800950

≡ *Hydropus mediterraneus* Pacioni & Lalli, Micol. Ital. 14(1): 5 (1985).
≡ *Flammulina mediterranea* (Pacioni & Lalli) Bas & Robich, Persoonia 13(4): 489 (1988).
≡ *Oudemansiella mediterranea* (Pacioni & Lalli) E. Horak, Riv. Micol. 31(1–2): 34 (1988).
≡ *Xerula mediterranea* (Pacioni & Lalli) Quadr. & Lunghini, Quad. Accad. Naz. Lincei 264: 112 (1990).
≡ *Xerula mediterranea* (Pacioni & Lalli) Ballero & Contu, Arch. bot. ital. 66(3–4): 148 (1990), comb. superfl.

Selected descriptions — Robich (1986: 199–202); Bas & Robich (1988: 489–494); Horak (1988: 31–37); Pancorbo & Ribes (2010: 290–291); Petersen & Hughes (2010: 514–515).

Selected iconography — Robich (1986: 201); Rocabruna (1988: 321); Ludwig (2001b: tab. 187, 89.3).

material studied: **ITALY**, **Lazio**, Latina, Parco Nazionale del Circeo, Sabaudia, coastal sand dunes, associated with *Ammophila littoralis*, 20 Nov 1977, leg. G. Pacioni, Flora Micologica del Circeo no. 402 (Holotype, AQUI 5273); **Tuscany**, Pisa, Parco Naturale Migliarino–San Rossore–Massaciuccoli, Vecchiano, Marina di Vecchiano, under *Juniperus macrocarpa*, 24 Nov 2008, leg. et det. M. Carbone (MCVE 23445); 12 Nov 2011, leg. et det. A. Pierotti (AP2011111204, TO AVP378).

Ecology & distribution: terrestrial, gregarious, associated with *Ammophila littoralis* and/or *Juniperus macrocarpa*/*J. phoenicea* in dune ecosystems. On the Italian Mediterranean coast, it is often typical of the *Ephedro fragilis-Juniperetum macrocarpae* Bartolo et al. vegetation association (Lantieri et al. 2009). Fruiting in winter. The species is saprobic probably on buried dead plant parts: Filippi (1991) reported for Tuscany dune collections a close association between the pseudorhizae (geopodia sensu Jacques–Félix 1967) and dead roots of *Juniperus macrocarpa* and *J. phoenicea*. Gonou-Zagou & Atsa (2011) refer to it as a possibly phoenicoid fungus whose growth and fruiting is stimulated after a fire. So far it is known from Mediterranean coastal dunes of Italy's east and west coasts (Sardinia and Sicily included) (Dal Savio 1984, Pacioni & Lalli 1985, 1986; Contu 1986, 1988, 2000; Robich 1986, Ballero & Contu 1990, Quadraccia & Lunghini 1990, Filippi 1991, Contu & Signorello 1999, Franchi et al. 2001, 2006; Monti et al. 2001, Lantieri et al. 2009, Bizio 2010), Spain and Balearic Islands (Rocabruna 1988, Ortega et al. 1991a, Siquier et al. 2009, Pancorbo & Ribes 2010, 2011), Greece (Gonou-Zagou & Atsa 2011), Tunisia (Pacioni & Lalli 1985, 1986), and from Atlantic coastal dunes of France (Guinberteau & Courtecuisse 1993, Guinberteau 2011) and Spain (Ortega et al. 1991a,b).

Discussion

Our ITS- and LSU-based phylogenetic analyses (Fig. 1) indicate the monospecific *Laccariopsis* as a new evolutionary line in *Physalacriaceae* where with *Gloiocephala* and *Rhizomarasmius* it forms the /gloiocephala clade, which is sister to the /xerula clade (*Strobilurus* and *Xerula*). These two clades were also informally pointed out by Binder et al. (2006).

Laccariopsis mediterranea is defined by a peculiar combination of macro- and micromorphological features, such as: 1) a clearly viscid, not striate pileus (often covered by strongly adhering sand particles); 2) distant and thick subdecurrent lamellae; 3) a strongly rooting stipe (incorporating plant debris and sand particles), pruinose only at apex, slightly viscid downwards; 4) long thin- to thick-walled spores, ellipsoid to subamygdaliform (11–16 × 8–11 µm); 5) long thin- to thick-walled basidia (52–80 × 10–14.5); 6) a pileipellis consisting of a loose ixohymeniderm with slender cylindrical to lageniform pileocystidia; 7) cheilo- and pleurocystidia protruding, thin- to thick-walled,

fusiform to lageniform; 8) thin- to slightly thick-walled and colourless septate caulocystidia confined to stipe apex; 9) a monomitic stipe trama; 10) abundant clamp-connections; 11) habitat in coastal dunes (our observations; and Bas & Robich 1988, Horak 1988, Contu 2000, Ludwig 2001a, Antonín & Noordeloos 2010, Pancorbo & Ribes 2010, Petersen & Hughes 2010).

Oudemansiella oreina Pacioni & Lalli (≡ *Xerula oreina* (Pacioni & Lalli) Contu), known only from the type collection from Simbruini Mountains, Abruzzi (Centre Italy) and not treated in Petersen & Hughes (2010), could possibly belong to *Laccariopsis*; it differs from *L. mediterranea* in having a collybioid/*Flammulina*-like habit (Bon 1999 considered it a *Flammulina*) with more crowded and non-decurrent lamellae, a striate pileus margin, a brown-purplish and entirely velutinous stipe, slightly smaller and strictly ellipsoid spores (9–14 × 7–9 µm), and growth in grass-covered mountain areas (Pacioni & Lalli 1989, Bon 1999, Contu 2000). Molecular data are needed to determine the taxonomic status of this species.

As regards morphological affinities at the generic level, *Laccariopsis, Gloiocephala,* and *Rhizomarasmius* (/gloiocephala clade) share a monomitic stipe trama (Redhead 1987, Horak & Desjardin 1994, Petersen 2000) and similar pileipellis structure and cystidia (Petersen 2000, Antonín & Noordeloos 2010). *Gloiocephala* differs in having basidiomes with a gracile marasmioid habit, a dry to subviscid pileus, a insititious to pseudoinsititious non-rooting stipe that is often short lateral or eccentric and usually entirely pruinose, a lamellate to reduced-smooth hymenophore, a dense hymeniform pileipellis, thin-walled spores, shorter and thin-walled basidia, and growth on herbaceous plant or wood leaves, stems, and debris, usually in wet places (Bas 1961, Redhead 1981, Singer 1986, Horak & Desjardin 1994, Desjardin et al. 1995, Antonín 2007, Tkalčec & Mešić 2008, Antonin & Noordeloos 2010). *Rhizomarasmius* is distinguished by basidiomes with a marasmioid habit, a dry pileus surface, a minutely and entirely pruinose-hairy stipe darkening downwards to brown-blackish, a ramified pseudorhiza (= rhizomorphic pseudorhiza sensu Norvell 1998), thin-walled spores, thin-walled shorter basidia, thin-walled hymenial cystidia, and a dense hymeniform pileipellis (Petersen 2000, Antonín & Noordeloos 2010, Ronikier & Ronikier 2011).

In the close /xeruloid clade, *Strobilurus* is characterized by a dry pileus surface, a stipe deeply rooting on buried hypogeous or superficial strobiles of conifers, on conifer wood, or on *Magnolia* fruits, a pileipellis consisting of a dense hymeniderm, thin-walled and shorter spores and basidia, a sarcodimitic stipe trama, and absence of clamp-connections (Wells & Kempton 1971, Redhead 1980, Singer 1986, Desjardin 1987, Noordeloos 1999, Gulden 2008). *Xerula* s.s. has a dry and velutinous pileus, an entirely velutinous-hispid rooting stipe, a pileipellis consisting of a dense hymeniderm with up to 1.5 mm long,

rigid and very thick-walled (≤6 µm thick) brown pileosetae, similar caulosetae, a sarcodimitic stipe trama, and clamp-connections (Petersen & Hughes 2010).

Finally, among the phylogenetically unrelated *Physalacriaceae,* the morphologically close genus *Flammulina* shares with *Laccariopsis* a viscid pileus, a similar pileipellis structure (in the extra European taxa), and a monomitic stipe trama, but differs in having a dry entirely velutinous stipe, well-developed pileocystidia, smaller and usually thin-walled spores and basidia, and usually thin-walled hymenial cystidia (Bas 1983, 1995; Redhead et al. 1999, 2000; Redhead & Petersen 1999, Ge et al. 2008, Petersen et al. 2012).

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